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COLD TEMPERATURE ADAPTATION IN THE RING-NECKED
PHEASANT, PHASIANUS COLCHICUS AND THE GRAY
PARTRIDGE, PERDIX PERDIX

BY



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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Cold Temperature Adaptation in the Ring-necked Pheasant, Phasianus colchicus and the Gray Partridge, Perdix perdix" submitted by Teresa May Delane, in partial fulfilment for the degree of Master of Science.

ABSTRACT

Seasonal changes in metabolism of acclimatized Ring-necked Pheasants and Gray Partridges were investigated to better understand the adaptation of these game birds to cold temperature. Metabolism was measured by the consumption of oxygen, in an open circuit respirometer. Food consumption, body weight, body temperature, and ambient temperature were also recorded in an attempt to correlate metabolic changes with environmental or morphological changes.

Lower temperature-metabolism slopes and lower critical temperatures during winter than during summer indicate seasonal acclimatization in both species. The mean standard metabolism was 0.66 cc $O_2/g/hr$ for pheasants and 1.16 cc $O_2/g/hr$ for partridges. Pheasants did not increase food consumption significantly in winter, but partridges did. There was no evidence for hypothermia at low ambient temperatures. Increased weight, decreased activity, and increased insulation were noted with the onset of cold weather. Body weight and food consumption varied with reproductive state as well as with ambient temperature per se.

Reproduction, molt, and low temperature are energetic stresses faced by pheasants and partridges at various times of the year. Although the winter period is stressful in regards to maintaining homeothermy and finding food, the birds are able to adapt to the cold. Added fat stores, decreased activity, and increased insulation are effective in reducing heat loss and ensuring survival of the species at this time.

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FOOTNOTES

1. Parr Instrument Co., Moline, Illinois, U.S.A.
2. Controlled Environments Ltd., Winnipeg, Manitoba, Canada.
3. Labline Instruments, Inc., Melrose Park, Illinois, U.S.A.
4. Manostat Corporation, New York, New York, U.S.A.
5. Beckman Instruments, Inc., Fullerton, California, U.S.A.
6. Hamilton Co., Whittier, California, U.S.A.
7. Yellow Springs Instrument Co., Ltd., Yellow Springs, Ohio, U.S.A.
8. Leeds & Northrup Co., Philadelphia, Pennsylvania, U.S.A.

INTRODUCTION

To test the effect of ambient temperature on metabolism, investigators have used both acclimated and acclimatized birds. Data from the former group indicate that low ambient temperatures result in (1) an increase in standard metabolic rate, (2) a slight downward shift in the thermoneutral zone, and (3) in most species, an extension of the limits of cold tolerance (King and Farner, 1961). Contrary to this, most species acclimatized to summer and winter seasons do not show differences in their standard metabolism or in their temperature-metabolism slopes (West, 1962). King and Farner (1961) suggest that this is because the temperature-conditioning process as found in acclimated birds is suppressed by the variable ambient temperatures encountered by acclimatized specimens. They also stress that in acclimatization experiments, factors other than temperature may be operating.

Since West's review of the adaptation of wild birds to environmental temperature in 1962, Hart (1962) also found no change in the seasonal temperature-metabolism slopes of the House Sparrow (Passer domesticus), Starling (Sturnus vulgaris), Pigeon (Columba livia), and Evening Grosbeak (Hesperiphona vespertina). Veghte (1964) did not observe a seasonal change in the standard metabolism of the Gray Jay (Perisoreus canadensis) but did note a lower temperature-metabolism slope during summer than during winter. Finally, Brush (1965) found no apparent seasonal changes in the standard metabolism of the California Quail (Lophortyx californicus).

Such data that exist on acclimatization in birds have been obtained mainly from passeriformes: Kendeigh (1949) and Davis (1955) for the House Sparrow; Wallgren (1954) for the Yellow Buntings (Emberiza spp.);

Rautenberg (1957) for the House Sparrow and Brambling (Fringilla montifringilla); Irving et al. (1955) for the Northwestern Crow (Corvus caurinus); Dawson (1958) for the Cardinal (Richmondena cardinalis); Hart (1962) for the House Sparrow, Evening Grosbeak, and Starling; and Veghte (1964) for the Gray Jay. The only non-passeriformes studied are the Black Brant (Branta nigricans; Irving et al., 1955), Pigeon (Hart, 1962), and California Quail (Brush, 1965).

In this study, oxygen consumption, body temperature, food consumption, and body weight of acclimatized Ring-necked Pheasants (Phasianus colchicus) and European or Gray Partridges (Perdix perdix) were measured over a one-year period to determine what seasonal changes, if any, occur in their metabolic responses to environmental temperature. These species were chosen mainly because of their easy availability, but also because they represent two of the most successful introductions of foreign game birds into Alberta.

Since their initial introductions in 1908, these birds have spread north as far as the Athabasca River in central Alberta (Mitchell, 1959). This latitude, in fact, represents the northern limits of both species in North America (Aldrich and Duvall, 1955). Weather, and particularly ambient temperature, has been linked with the success of introduced game birds (Graham and Hesterberg, 1948; McCabe and Hawkins, 1946; Porter, 1955). Thus, a study on the seasonal acclimatization of pheasants and partridges does not only add to the knowledge of thermoregulation in large birds. It also provides information which is pertinent to the winter ecology of these game species and is applicable to management practices as far as distribution and numbers are concerned.

MATERIALS AND METHODS

Maintenance of Birds

Adult pheasants and partridges were obtained from the Alberta Government Pheasant Hatchery at Brooks, Alberta. They were acclimatized in outdoor wire pens at the University of Alberta Farm, Edmonton. One pen of 1174 ft² with a shed of 168 ft² housed 8 partridges during the summer of 1967 and 4 throughout the rest of the year. The number of pheasants varied from 6 in the summer of 1967, 12 during the fall, 11 during the winter, and 8 in the spring of 1968. During the summer of 1967 the pheasants were allowed approximately 686 ft² of pen per bird, plus a shed of 168 ft². This area was reduced to approximately 268 ft² per bird during the fall and winter, and in spring increased to about 513 ft² per bird.

From June, 1967 to December, 1967, inclusive, all birds were maintained on Master 18 per cent layer mash (18% protein, min.; 3.5% fat, min.; 5.5% fiber, max.) obtained from the Brooks Pheasant Hatchery. During January, 1968, the birds were fed Vigor Feeds Pheasant Grower (20% protein, min.; 3.0% fat, min.; 8.0% fiber, max.) also from the Brooks Pheasant Hatchery. In all subsequent months North West Mill & Feed Co., Ltd. 20 per cent Turkey Grower (20% protein, min.; 3.5% fat, min.; 8.5% fiber, max.) was provided. Undoubtedly, all birds supplemented their diets in the summer with invertebrates and green plants found within their pens. Water was provided when snow was not present.

As temperature falls, and as metabolism increases, one would expect energy intake to increase. To determine food consumption the volume

of food remaining in the feeding pans was measured and converted to a weight value. The feeding pans were constructed to minimize loss of food. Daily food consumption was measured for both male and female pheasants, and their weights were also recorded separately. Since the weights of male and female partridges do not differ greatly throughout most of the year (Westerskov, 1965), their food consumption and average weights were combined except for the months of June, 1967, and May, 1968, when the weights were expressed separately.

To determine gross caloric intake, the caloric content of the various food pellets was measured in an adiabatic calorimeter¹. The material was first dried at 70 C for 72 hours. Because all the faeces were not collected and weighed, it was impossible to determine net caloric intake; that is, gross energy minus indigestible energy. Nor was it possible to investigate seasonal changes in digestive efficiency. These problems must be examined for a more accurate study of the seasonal energy balance in these birds.

The Department of Transport supplied weather records from the Edmonton International Airport meteorological station. Data from this station (Appendix IV) average one to two degrees lower than those from the Edmonton city station, but were used here since the pens were located in an open field, approximately 100 yards from the nearest heated building.

Measurement of Metabolic Rate

Theoretically, the best determination of metabolic intensity is the direct measurement of heat liberated from a subject under appropriate

standard conditions. This, however, requires relatively elaborate instrumentation, and for simplicity, indirect calorimetry has been more widely used (King and Farner, 1961). This technique is based on the fact that oxygen consumption and carbon dioxide production are closely correlated with heat production, and relationships have been determined which allow the estimation of heat production from the measured respiratory exchange.

A "temperature-metabolism curve" depicts metabolism as a function of temperature. The bottom of the U-shaped curve lies in the thermoneutral zone, that range of temperatures within which metabolism is minimum or "standard". As temperature decreases, metabolism increases, and the relationship can be plotted as a regression line. The lower critical temperature marks the lower end of the thermoneutral zone, and is taken as the point at which each of the regression lines intersect the mean standard metabolic rate. Metabolism also increases beyond the upper critical temperature, but this relationship was not investigated as I was interested only in the adaptation of pheasants and partridges to cold temperatures.

Metabolic rate was measured by an open circuit method for determining oxygen consumption. The birds were placed in plexiglas chambers, two of 21 liters each and a third of 56 liters, which were inside a controlled temperature cabinet² (Fig. 1). Temperatures in this cabinet could be controlled automatically or manually within a range of -40 C to +40 C.

The system consists of three air-flow circuits, providing alternate recording from three birds during a particular experimental session (Fig. 2).

In the main circuit, air from one of the chambers is drawn by a pump through a wet-test gas flowmeter³ and a predictability flowmeter⁴. From this circuit some air can be diverted at a reduced flow rate to the Beckman Model E2 paramagnetic oxygen analyzer⁵. This sample air is first dried in a tube of anhydrous CuSO₄ ("Drierite"), filtered through cotton, and its flow rate measured by a predictability flowmeter. Also entering the sample circuit are standard gases (100 per cent nitrogen and 100 per cent atmosphere) for calibration of the analyzer. Finally, an auxiliary circuit, with a third predictability flowmeter, ensures that the air flow from the other two chambers is maintained while the first is being sent through the sample circuit. Manual manipulation of air-tight luer-lock connectors⁶ allows the air from each chamber to be successively measured in the sample circuit.

The flow rate in the main circuit was set between 900 and 1500 cc/min to ensure an oxygen content of more than 17 per cent and carbon dioxide content of less than 4 per cent in the air leaving the animal chamber. To calculate oxygen consumption, the following formula from Depocas and Hart (1957) was used:

$$V_{O_2} = V_E \frac{(\%I_{O_2} - \%E_{O_2})}{100}$$

Where V_{O_2} = oxygen consumption in cc O₂/min;

V_E = flow rate of outlet gas in cc/min;

$\%I_{O_2}$ = per cent oxygen of inlet gas (assumed 20.9 per cent); and

$\%E_{O_2}$ = per cent oxygen of outlet gas.

Gas volumes were not corrected to standard conditions of temperature and pressure. They were measured at a temperature of 22-25 C and a

Figure 1. Controlled temperature cabinet with plexiglas chambers.
Arrows indicate direction of air flow. Tubing passes
out of cabinet to analysis equipment.

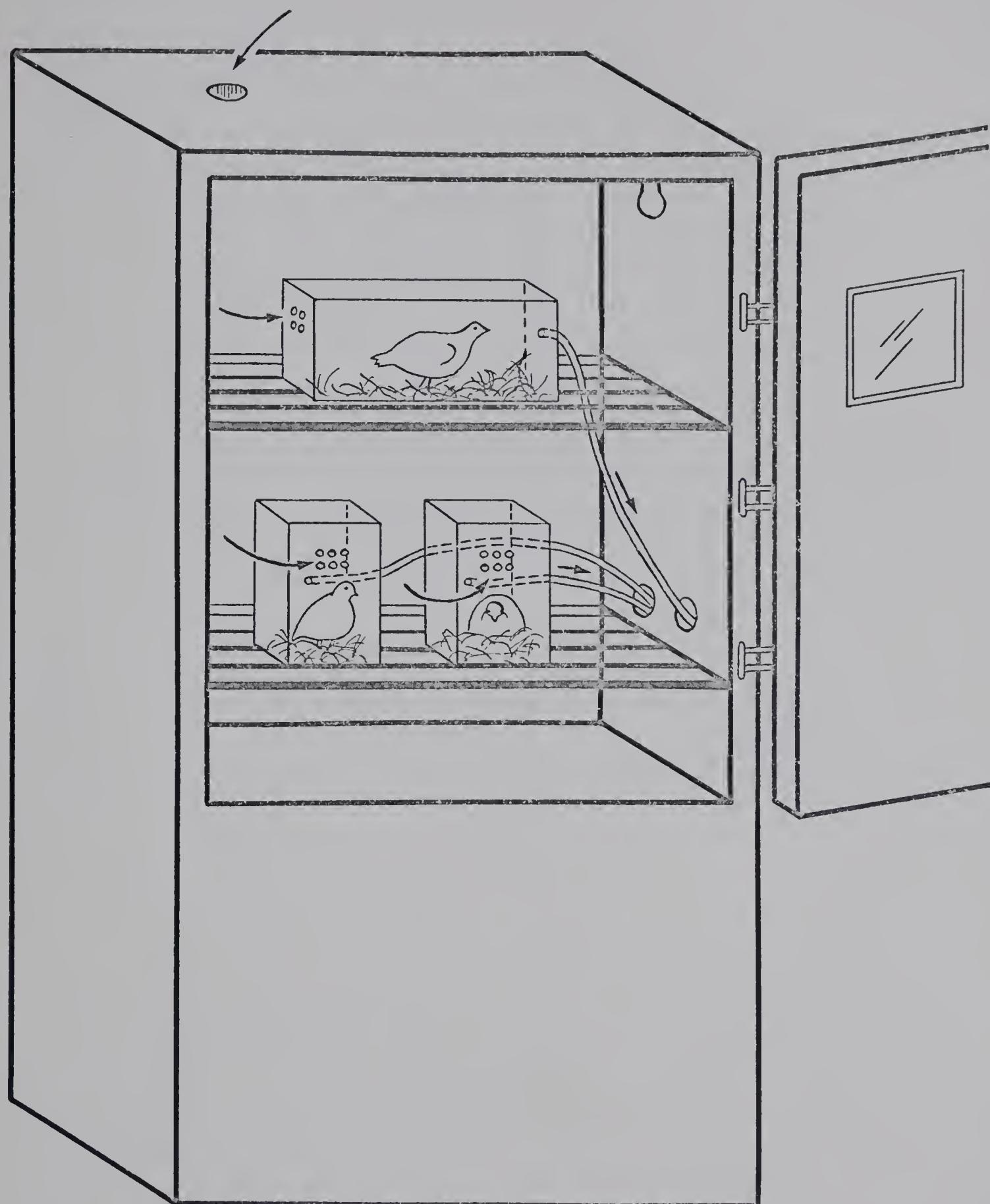
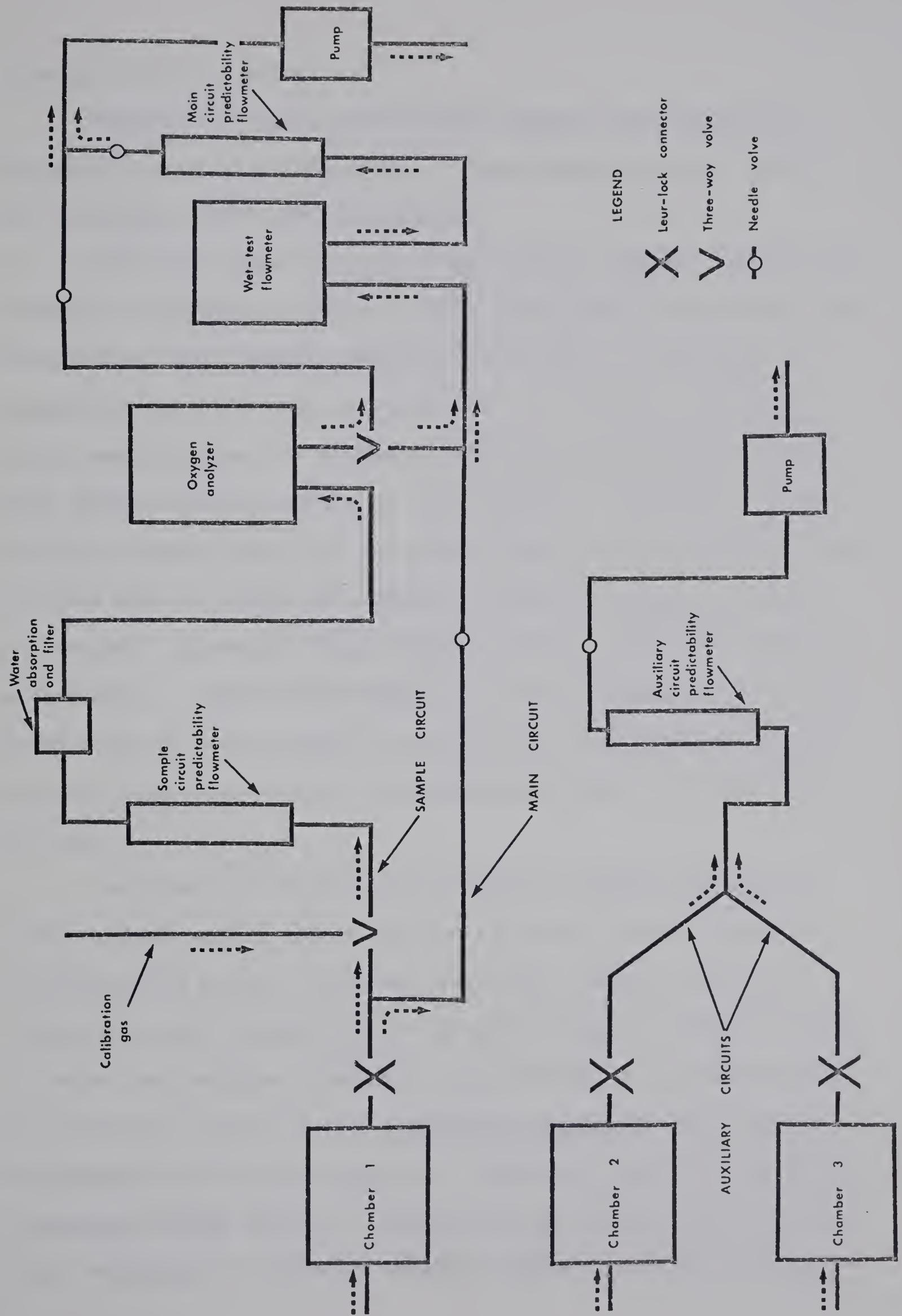


Figure 2. Main, sample, and auxiliary respirometry circuits. Air flow indicated by broken arrows. Luer-lock connectors allow chambers and circuits to be interchangeable.



pressure of 685-715 mm Hg.

Temperatures within the individual chambers were monitored by thermistors and a tele-thermometer⁷. These temperatures were used in all comparisons with oxygen consumption.

Birds were taken from pens in the morning, weighed, placed in the chambers, and allowed to adjust to their surroundings for at least three hours before their oxygen consumption was measured. Partridges were weighed to the nearest gram and pheasants to the nearest ten grams on triple beam balances. To facilitate handling, the pheasants were hooded. They quickly became accustomed to this procedure. Partridges, however, would not tolerate hoods and thus their heads were left uncovered. Pieces of black plastic between the chambers prevented the birds from seeing one another. Although darkened chambers may have calmed the birds more effectively, a light in the temperature cabinet remained on so that the birds could be viewed through a one-way mirror. Any measurements taken when the birds were observed to be excessively active or excited were not used.

The three hours allowed for the birds to become accustomed to their chambers was not sufficient time for them to become completely post-absorptive as well. Kaup and Ivey (1923) reported that four to twelve hours were required for food to pass through the digestive tract of fowls, and Pendergast (personal communication) in a present study on the nutrition of Spruce Grouse (Canachites canadensis) finds that approximately four hours are required. Therefore, in addition to regular experiments during the day, I conducted several 24-hour runs at a constant temperature to determine possible changes in metabolism as the

birds became post-absorptive.

The terms "summer", "fall", "winter", and "spring" as used in this study represent periods of the year, chosen on the basis of seasonal weather changes, during which oxygen consumption and food consumption were measured. In all tables referring to oxygen consumption, "summer" was July and August, 1967; "fall" was November, 1967; "winter" was January and February, 1968; and "spring" was April, 1968.

Concurrent with the measurement of oxygen consumption, the body temperature of any one bird, as well as cabinet, chamber, and room temperatures could be measured on a multipoint recorder⁸. For body temperature, a 30-gauge copper-constantan thermocouple wire, its end smoothed with a plastic coating, was inserted two inches into the bird's cloaca and large intestine and fastened to tail feathers with light-weight clips. The other temperatures were monitored by 20-gauge copper-constantan wires.

Statistical Analysis

Student's t-test for unpaired means was used to determine statistical significance of differences in monthly food consumption and seasonal standard metabolism (Steel and Torrie, 1960). Regression equations for the data of oxygen consumption versus temperature were calculated by the method of least squares (Croxton, 1953).

RESULTS

OXYGEN CONSUMPTION

Temperature-metabolism Curves

Figure 3 and Appendices I and II depict the seasonal changes in the relationship of environmental temperature to the metabolism of pheasants and partridges, as determined from oxygen consumption. In calculating the regression equations (Table 1) only those points falling below 10 C were used; this temperature appeared to be the point of inflection of the curves. Likewise, metabolism seemed to be fairly constant between 10 C and 30 C and therefore this was considered as the thermoneutral zone. The slopes of the curves during summer, fall, and spring for pheasants are essentially the same, although the former is on a higher level than the latter two. Winter metabolism for these birds is represented by a horizontal line, i.e., metabolism is more or less constant from 30 C to -40 C, with no rise at temperatures below the thermoneutral zone. For the partridges, the slope is greatest in fall, approximately equal in spring and summer, and lowest in winter.

Temperature-metabolism curves can also be determined theoretically, and compared with those found by experimentation (Figs. 4 and 5). Standard metabolism is predicted from an equation for non-passerine birds (Lasiewski and Dawson, 1967). Slope is predicted from the thermal conductance equation of Lasiewski et al. (1967). Thermal conductance is defined as the slope of increasing metabolism with decreasing ambient temperature below the thermoneutral zone, and is expressed as a positive value: cc O₂/g/hr/°C. It represents total heat loss through avenues of

evaporation, conduction, convection, and radiation, and a low thermal conductance value indicates high resistance to heat flow. The line of thermal conductance is drawn to intersect zero metabolism at the mean body temperature of the species.

TABLE I. Seasonal regression equations for pheasants and partridges, as determined from the method of least squares.

Season	Pheasants	Partridges
Summer	$Y = 1.26 - 0.022t$ $r = -0.64$ $N = 31$ $S_E = 0.28$	$Y = 1.77 - 0.020t$ $r = -0.51$ $N = 39$ $S_E = 0.44$
Fall	$Y = 0.97 - 0.020t$ $r = -0.86$ $N = 26$ $S_E = 0.14$	$Y = 1.47 - 0.041t$ $r = -0.92$ $N = 16$ $S_E = 0.24$
Winter	$Y = 0.93$ $N = 35$	$Y = 1.64 - 0.016t$ $r = -0.54$ $N = 27$ $S_E = 0.28$
Spring	$Y = 0.88 - 0.022t$ $r = -0.82$ $N = 27$ $S_E = 0.20$	$Y = 1.71 - 0.024t$ $r = -0.48$ $N = 26$ $S_E = 0.51$

Symbols used: Y = cc O_2 /g/hr; t = temperature, $^{\circ}C$; r = correlation coefficient; N = number of observations; S_E = standard error of estimate.

Body Temperature

In general, body temperatures of both pheasants and partridges were found to fall when the birds were active at low ambient temperatures but tended to rise slightly if the birds remained quiet at the same low

Figure 3. a. Observed seasonal temperature-metabolism curves of pheasants. The horizontal line of winter metabolism ($0.93 \text{ cc } O_2/\text{g/hr}$) is the mean of all points between -40° C and $+30^\circ \text{ C}$. The value for standard metabolism alone, between 10° C and 30° C , is somewhat lower, $0.87 \text{ cc } O_2/\text{g/hr}$.

b. Observed seasonal temperature-metabolism curves of partridges.

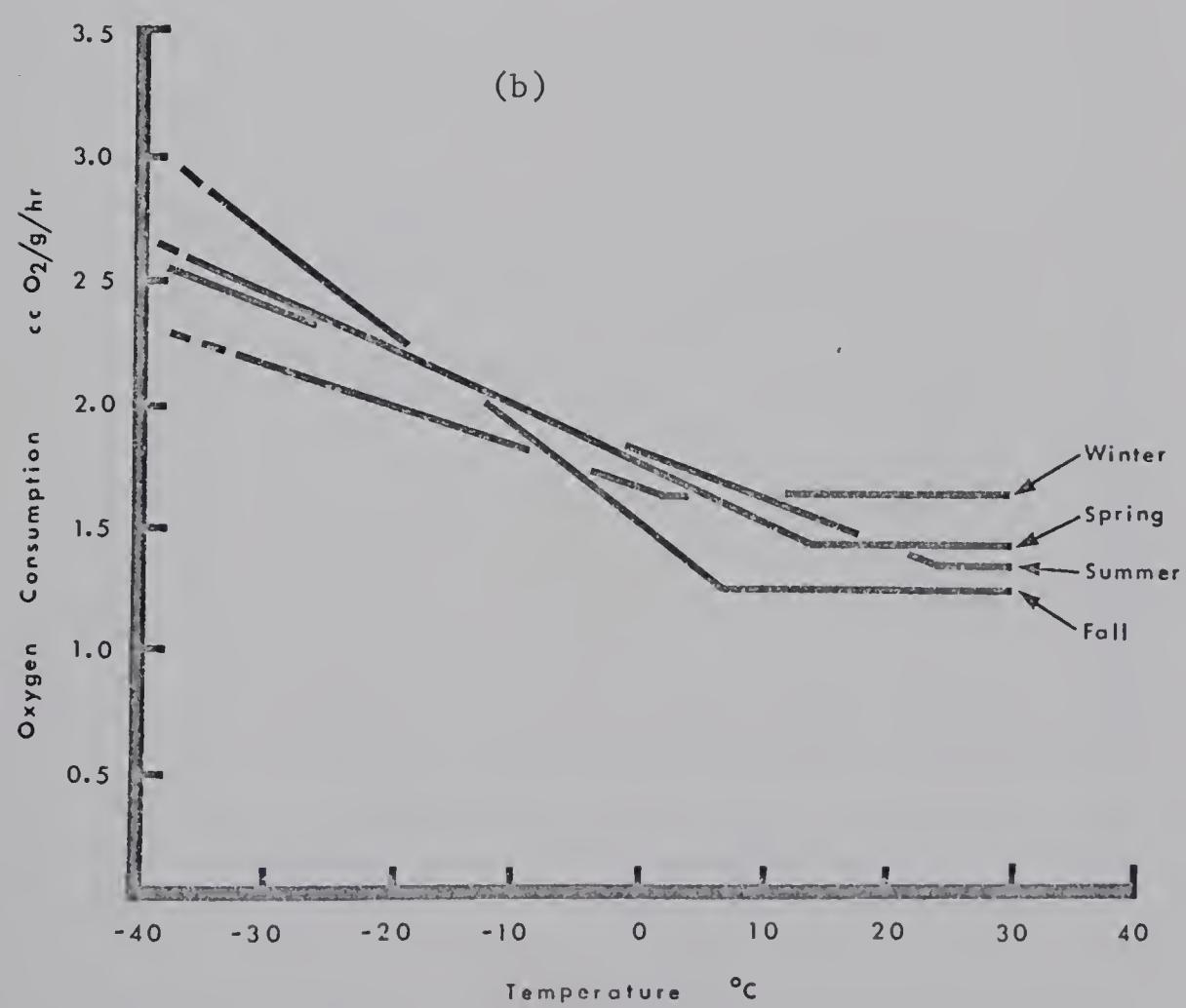
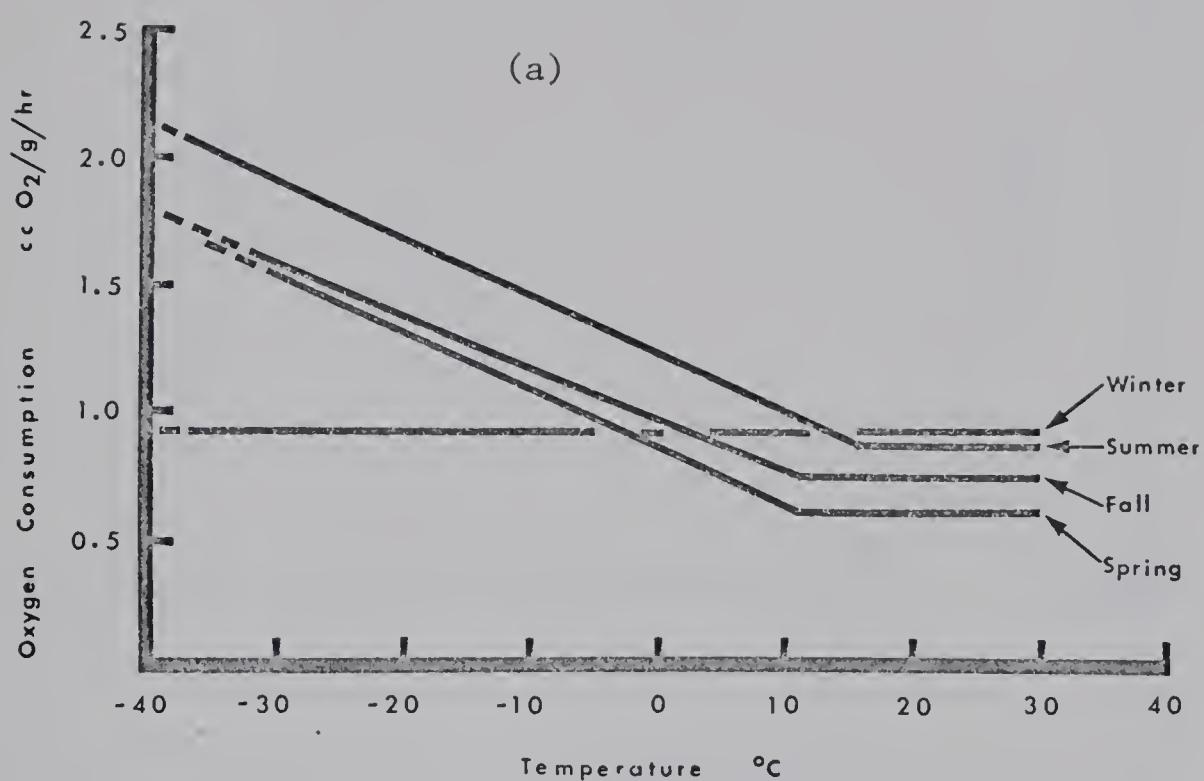


Figure 4. Predicted and observed seasonal temperature-metabolism curves of pheasants. Dots represent observed data of oxygen consumption. Solid line in thermoneutral zone represents the mean of values in this range; solid line below thermoneutrality is fitted by method of least squares. Broken line in thermoneutral zone is standard metabolism as predicted by equation of Lasiewski and Dawson (1967); broken line below thermoneutrality is calculated from thermal conductance equation of Lasiewski et al. (1967) and is drawn to intersect zero metabolism at body temperature of 43.0 C.

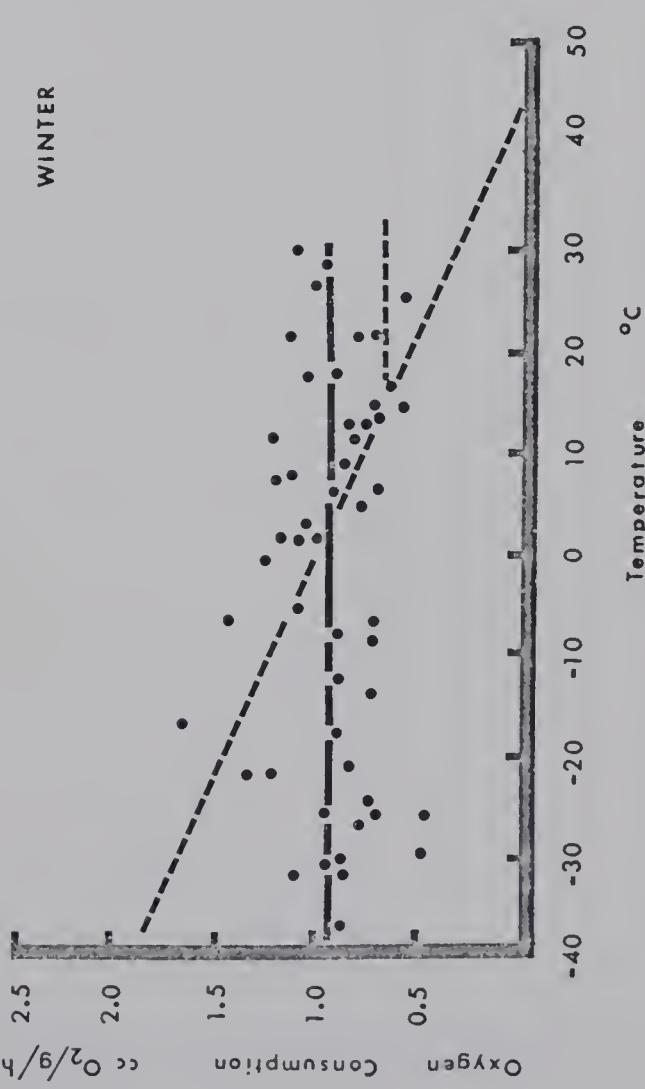
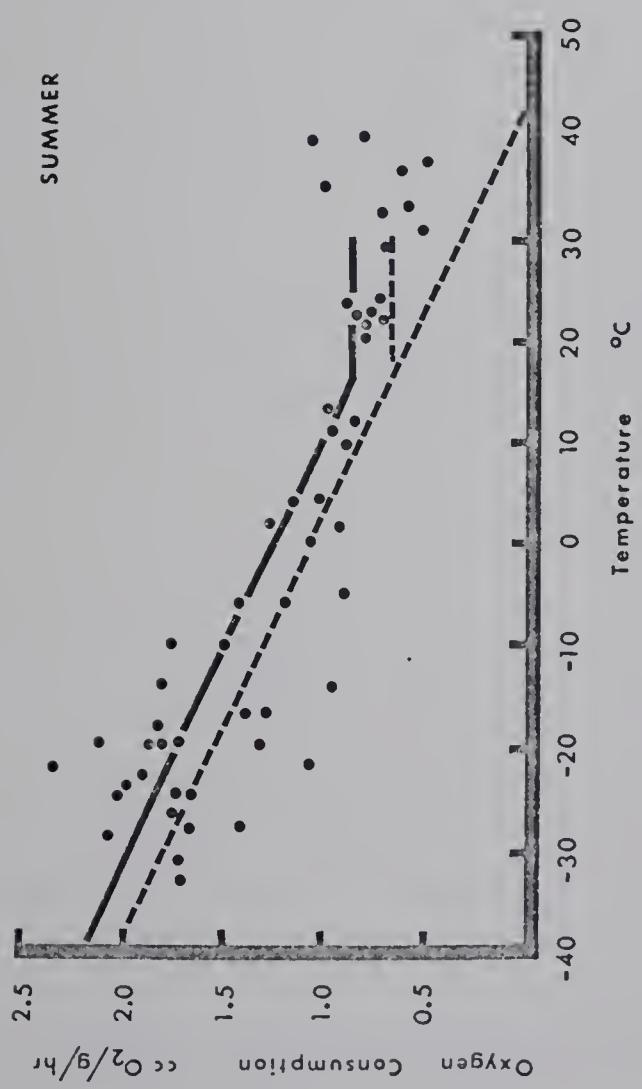
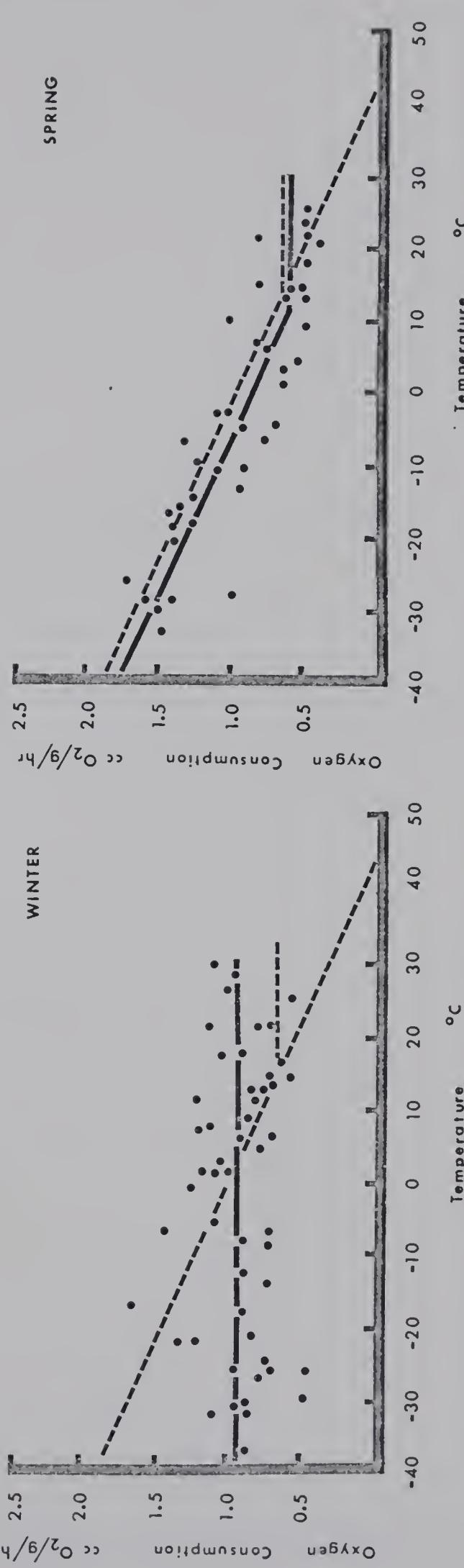
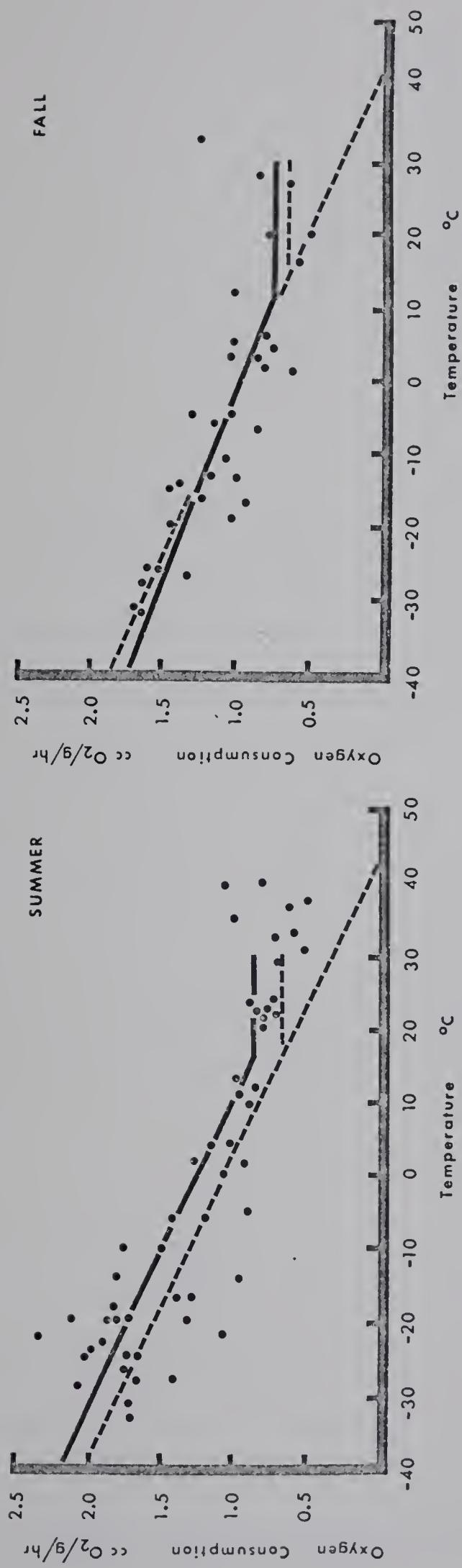
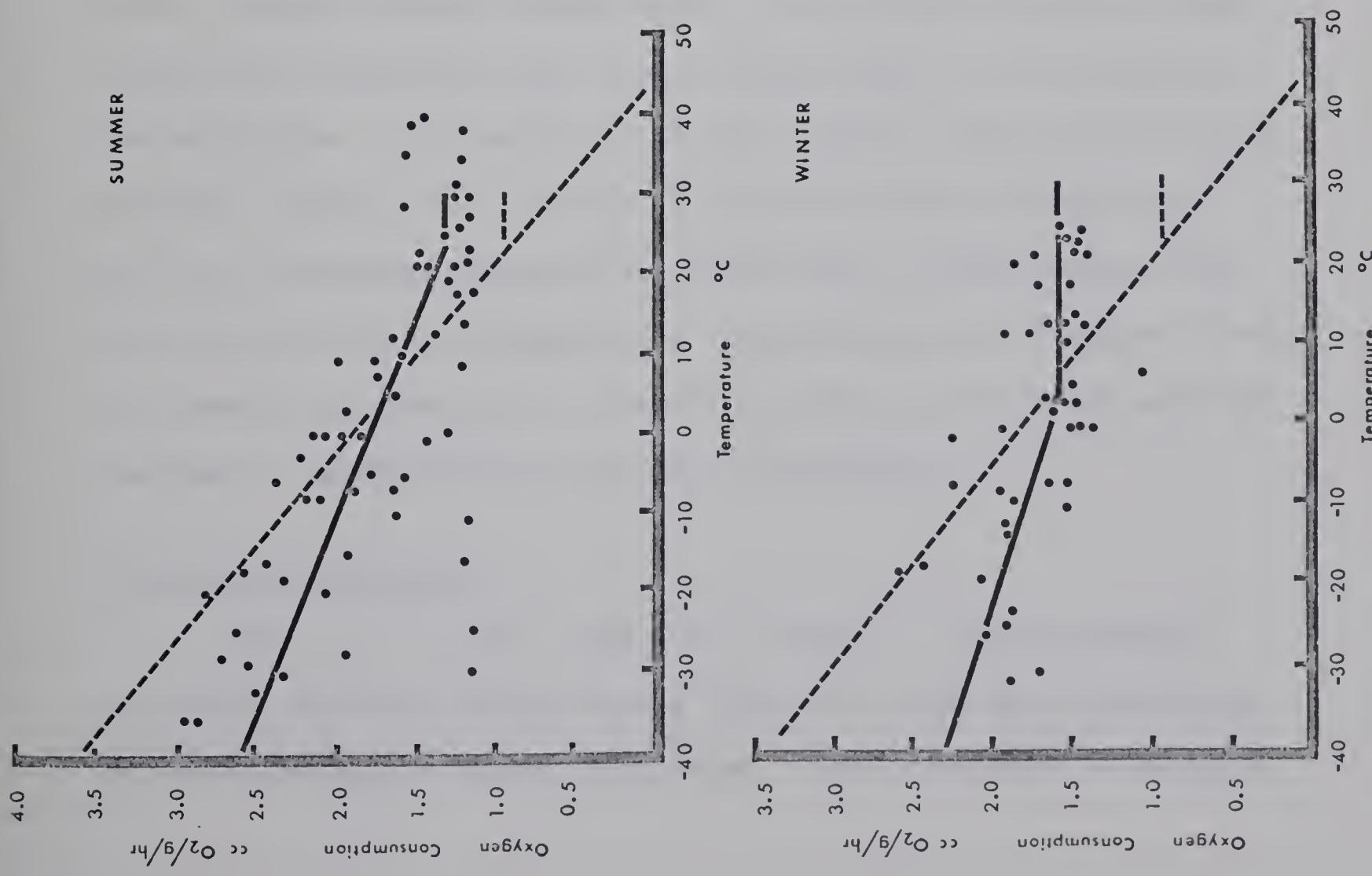
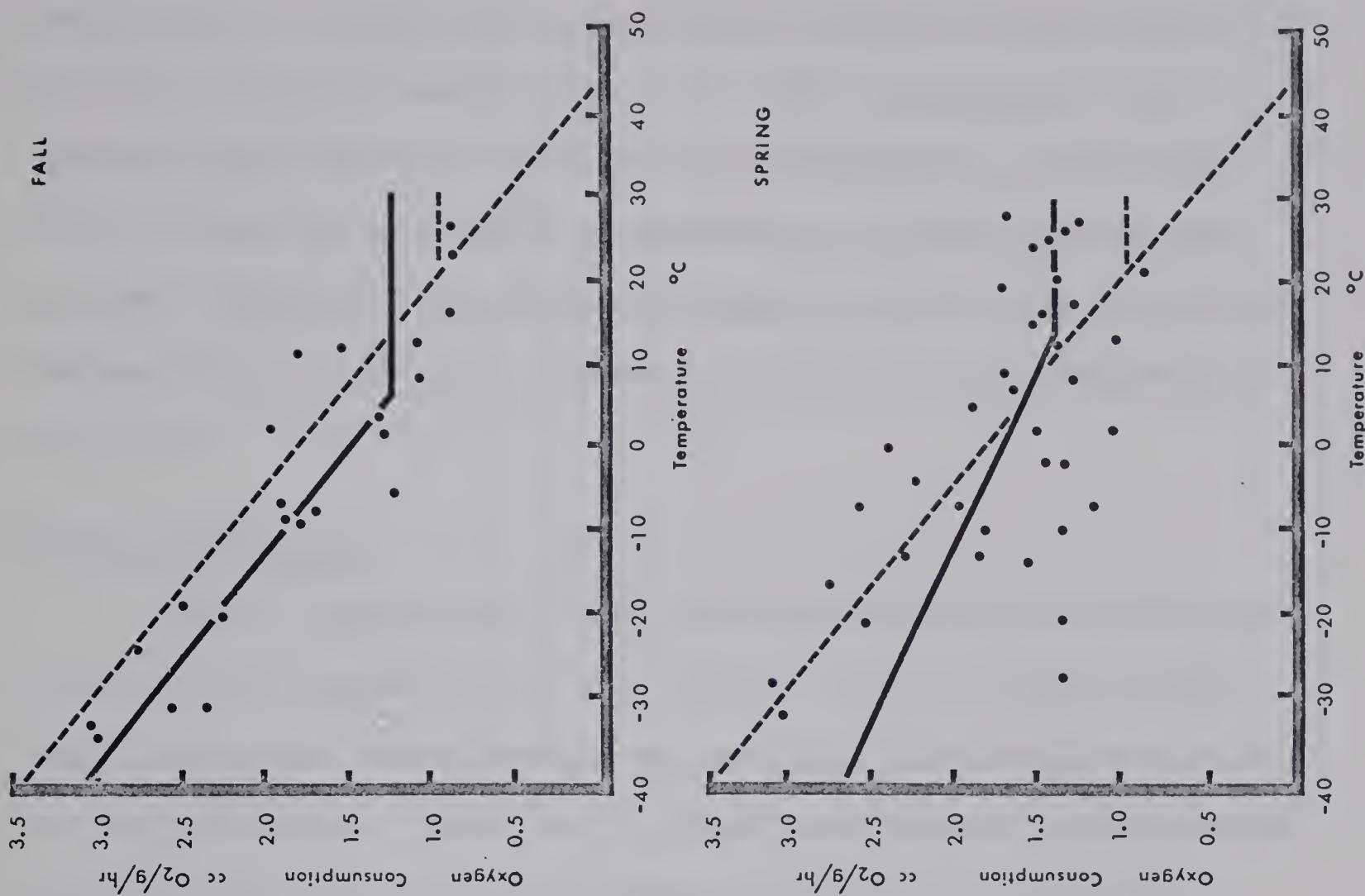


Figure 5. Predicted and observed seasonal temperature-metabolism curves of partridges. Dots represent observed data of oxygen consumption. Solid line in thermoneutral zone represents the mean of values in this range; solid line below thermoneutrality is fitted by method of least squares. Broken line in thermoneutral zone is standard metabolism as predicted by equation of Lasiewski and Dawson (1967); broken line below thermoneutrality is calculated from thermal conductance equation of Lasiewski et al. (1967) and is drawn to intersect zero metabolism at body temperature of 43.5 C.



temperatures. Although body temperatures of pheasants ranged from 37.5 C to 45.0 C, they were usually near 43.0 C. Body temperatures of partridges ranged from 42.0 C to 44.0 C but were generally recorded near 43.5 C. There was no evidence of hypothermia at lowered ambient temperatures. Therefore, this phenomenon cannot be used to help explain the failure of the metabolism of pheasants to rise at low temperatures during winter.

Thermal Conductance

Table II compares the observed and predicted thermal conductance values for all seasons and for both species. As can be seen from this table, the seasons during which theory and observation comply most closely are fall and spring. These are the transitional times of a summer-winter seasonal study and are the months of the year when the birds are at their "average" weights (Appendix IV). The greatest deviation between observed and predicted slopes occurs during winter for both pheasants and partridges. It is essential to note, however, that the theoretical equations depend solely upon the parameter of weight and therefore, I feel, may adequately represent the birds only at certain times of the year or under certain circumstances. For instance, no allowance is made for metabolic, behavioral, or insulative variations which may occur in response to environmental or endogenous influences.

Behavior and Insulation

Kabat et al. (1956) noted that in winter, if food is readily available, pheasants generally move very little each day, often merely between roosting and feeding localities. Such curtailment of activity

was noted in this study both in the outdoor pens and in the respirometer chambers. In the latter, it was especially noted that at all experimental temperatures both species became quiet very quickly and usually remained immobile throughout the course of the experiment. This was in contrast to other seasons, when the birds often required four to five hours before they quieted appreciably, and when bursts of activity alternated with periods of inactivity at low temperatures.

TABLE II. Comparison of observed and predicted thermal conductance values (cc O₂/g/hr/°C) during the year for pheasants and partridges. Predicted from the thermal conductance equation of Lasiewski et al. (1967).

Season	Pheasants		Partridges	
	Observed	Predicted	Observed	Predicted
Summer	0.022	0.024	0.020	0.043
Fall	0.020	0.023	0.041	0.042
Winter	-	0.023	0.016	0.041
Spring	0.022	0.022	0.024	0.042

Since pheasants molt only once a year, in late summer and early fall (Bent, 1932), no gross changes in insulation would be expected between summer and winter, except for the formation of a brood patch on the female. Insulation would vary only with the degree of feather erection. In contrast, partridges undergo two molts, a partial prenuptial molt in May and June and a complete postnuptial molt from July to November (Bent, 1932). A 16 per cent increase in plumage weight from summer to winter has been noted in this species (Westerskov, 1965).

The above behavioral and insulative variations are physical means of thermoregulation. That is, they are mechanisms employed to increase the total insulation of the body before an increase in heat production is required, and their effect is to extend the lower critical temperature.

Lower Critical Temperature

The observed lower critical temperature of pheasants is highest in summer, lower in fall and spring, and apparently entirely absent in winter over the range of temperatures studied (Table III). For partridges, the lower critical temperature is highest in summer, lower in fall and spring, and lowest in winter. Comparison of lower critical temperatures as determined by the least squares method and by the application of theoretical curves reveals similar values for summer birds but very different values for winter birds. Although lower critical temperatures during winter indicate seasonal acclimatization, it must be remembered that the experimental data (Figs. 4 and 5) show a gradual transition from physical to chemical thermoregulation over a span of about ten degrees without a sharply defined critical temperature. That is, as ambient temperature falls below thermoneutrality, the bird shifts from insulative modifications (vasoconstriction of peripheral vessels, increased insulating ability of the plumage, huddling) to higher heat production (exercise, increased muscle tone, shivering). Therefore, critical temperatures should, as Veghte (1964) points out, be considered only a rough but useful indication of metabolic acclimatization.

TABLE III. Comparison of lower critical temperatures ($^{\circ}\text{C}$) for pheasants and partridges as determined by the least squares method and from the theoretical curves of Lasiewski and Dawson (1967) and Lasiewski et al. (1967).

Season	Pheasants		Partridges	
	Least squares	Theoretical	Least squares	Theoretical
Summer	16	15	24	22
Fall	11	14	7	21
Winter	--	13	3	21
Spring	11	14	14	22

Standard Metabolism

Except for pheasants in spring, the observed standard metabolism at all seasons and for both species are higher than those predicted (Tables IV and V). This likely results from the failure of the birds to become completely at ease in the respirometer chambers (although often they were observed to be sleeping or preening), or to attain a true post-absorptive state within the time limits of the experiments. King and Farner (1961) report that increased levels of nutrition raise the standard metabolism and decrease the lower critical temperature. Although no study has thoroughly investigated this matter in birds, Webster (1967) reports that heat production in sheep is increased some 22.6 per cent by feeding. My investigations indicate that after twenty-four hours the metabolism of pheasants drops approximately 14 per cent and partridges, 24 per cent (Fig. 6). If the observed values for standard metabolism are lowered by these proportions, they correspond more closely

to predicted values. Also, if gas volumes are corrected to standard temperature and pressure, the values are closer to those predicted (Tables IV and V). For the purpose of interspecific comparison, the values of 0.66 cc O_2 /g/hr for pheasants and 1.16 cc O_2 /g/hr for partridges should be used. These are corrected to standard temperature and pressure only since most investigators do not wait 24 hours for their birds to become post-absorptive. The only significant change in standard metabolism of pheasants is the decrease observed from winter to spring (D.F. = 27, $t = 3.62$, $P < 0.05$). Standard metabolism of partridges also decreases significantly from winter to spring (D.F. = 28, $t = 3.01$, $P < 0.05$), and, in contrast to pheasants, exhibits a significant increase from summer to winter (D.F. = 36. $t = 6.00$, $P < 0.05$).

TABLE IV. Comparison of observed and predicted standard metabolic rates (cc O_2 /g/hr) of pheasants. Predicted values are from the equation of Lasiewski and Dawson (1967) for non-passerines, based on weight and assuming a conversion factor of 4.7 kcal/liter O_2 /day. Observed values are corrected for a post-absorptive state and to standard temperature and pressure.

Season	Observed			Corrected	Corrected	Av. wt. (Kg)
	Original	SD	N	for post- abs. state	to STP	
Summer	0.88	0.06	12	0.76	0.75	0.68
Fall	0.75	0.18	6	0.64	0.64	0.66
Winter	0.87	0.19	17	0.75	0.74	0.66
Spring	0.62	0.18	12	0.53	0.53	0.64
\bar{X}	0.78			0.67	0.66	1.189

Symbols used: SD = standard deviation; N = number of observations; \bar{X} = mean.

TABLE V. Comparison of observed and predicted standard metabolic rates (cc O₂/g/hr) of partridges. Predicted values are from the equation of Lasiewski and Dawson (1967) for non-passerines, based on weight and assuming a conversion factor of 4.7 kcal/liter O₂/day. Observed values are corrected for a post-absorptive state and to standard temperature and pressure.

Season	Original	SD	N	Corrected for post- abs. state	Corrected to STP	Predicted	Av. wt. (Kg)
Summer	1.29	0.16	21	0.98	1.10	0.93	0.355
Fall	1.21	0.42	5	0.92	1.03	0.91	0.370
Winter	1.59	0.14	17	1.21	1.25	0.90	0.394
Spring	1.37	0.23	13	1.04	1.16	0.91	0.378
\bar{X}	1.36			1.04	1.16	0.91	0.374

Symbols used: SD = standard deviation; N = number of observations; \bar{X} = mean.

FOOD CONSUMPTION

Food Consumption and Body Weight in Relation to Ambient Temperature

An increase in energy intake with decreasing ambient temperatures has been found in all small wild birds studied so far (King and Farner, 1961; West, 1962; Hart, 1962). It has also been found (Kabat et al., 1956; Westerskov, 1965) that pheasants and partridges increase their weight with the onset of colder temperatures in the fall.

Tables VI, VII, VIII, and IX, and Appendices III and IV record the caloric content of food pellets, gross food consumption, and body weight of pheasants and partridges from June, 1967 to May, 1968. Each caloric value of the food pellets is a mean of two determinations, each of which was within seven per cent of the mean.

Figure 6. Drop in metabolism over a 24-hour period, with artificial photoperiod (17 hours light, 7 hours dark) and temperature set at 15 C. Partridge #256; May 30-31, 1968. Data points during those periods when there were no changes in oxygen consumption have not been included.

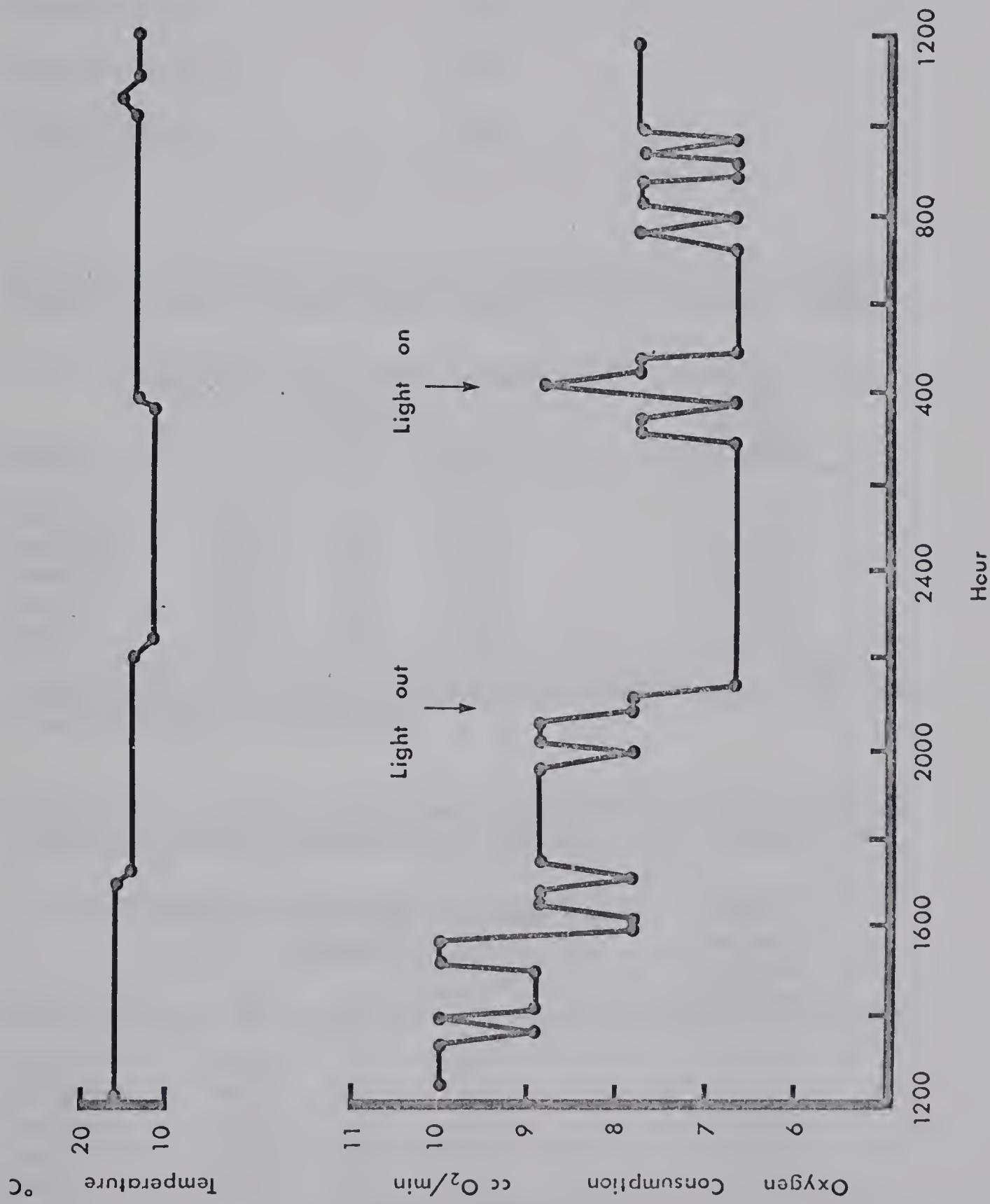


TABLE VI. Caloric value of the food pellets.

Feed	Caloric content (kcal/g)
Pheasant layer	4.233
Pheasant grower	4.331
Turkey grower	4.236

TABLE VII. Average daily food consumption and daily caloric intake for male pheasants from August, 1967 to April, 1968.

Month	Average daily food consumption (g/day)			Daily caloric intake (kcal/day)
	\bar{X}	N	$2\sigma_{\bar{X}}$	
August	49.0	5	13.3	207.27
November	64.3	21	3.1	271.66
January	58.3	17	2.5	252.34
March	70.1	19	3.2	297.21
April	73.4	19	7.8	311.60

Symbols used: \bar{X} = mean; N = number of observations; $2\sigma_{\bar{X}}$ = two standard errors of the mean.

TABLE VIII. Average daily food consumption and daily caloric intake for female pheasants from August, 1967 to April, 1968.

Month	Average daily food consumption (g/day)			Daily caloric intake (kcal/day)
	\bar{X}	N	$2\sigma_{\bar{X}}$	
August	49.0	5	13.3	207.27
November	40.2	21	3.2	173.15
January	40.0	15	8.4	173.01
March	44.2	19	12.3	187.28
April	56.6	16	6.2	240.04

Symbols used: \bar{X} = mean; N = number of observations; $2\sigma_{\bar{X}}$ = two standard errors of the mean.

TABLE IX. Average daily food consumption and daily caloric intake for partridges from August, 1967 to April, 1968.

Month	Average daily food consumption (g/day)	N	$2\sigma_{\bar{X}}$	Daily caloric intake (kcal/day)
August	21.9	5	2.5	92.84
November	30.0	7	1.8	139.91
December	29.4	10	2.1	124.22
January	35.8	19	5.2	154.81
March	23.6	20	2.0	100.08
April	31.8	19	4.6	135.01

Symbols used: \bar{X} = mean; N = number of observations; $2\sigma_{\bar{X}}$ = two standard errors of the mean.

Gross caloric intake does not vary inversely with temperature for pheasants but does for partridges. In addition, food consumption does not increase significantly from summer (August) to winter (January) for pheasants, but does for partridges. This may be because of the smaller size of partridges. Body heat may be lost more quickly at low ambient temperatures, thus necessitating higher food consumption. Body size and rate of heat loss are also involved in the lower oxygen consumption (per gram body weight) of pheasants, especially during winter. All birds show significant increases of food consumption in spring - January to March for male pheasants, January to April for female pheasants, and March to April for partridges. This could be due to the maturation of gonads and initiation of reproductive activities, as well as to a general increase in activity associated with higher ambient temperatures. Table X indicates t values and degrees of freedom for all significant changes in food consumption from month to month. Figures 7, 8, and 9 depict changes in ambient temperature, body weight, and gross food consumption of pheasants and partridges from June, 1967 to May, 1968.

Figure 7. Mean monthly body weight (solid line), mean monthly ambient temperature (broken line), and average daily food consumption (squares) of male pheasants from June, 1967 to May, 1968. Vertical bars represent two standard errors of the mean.

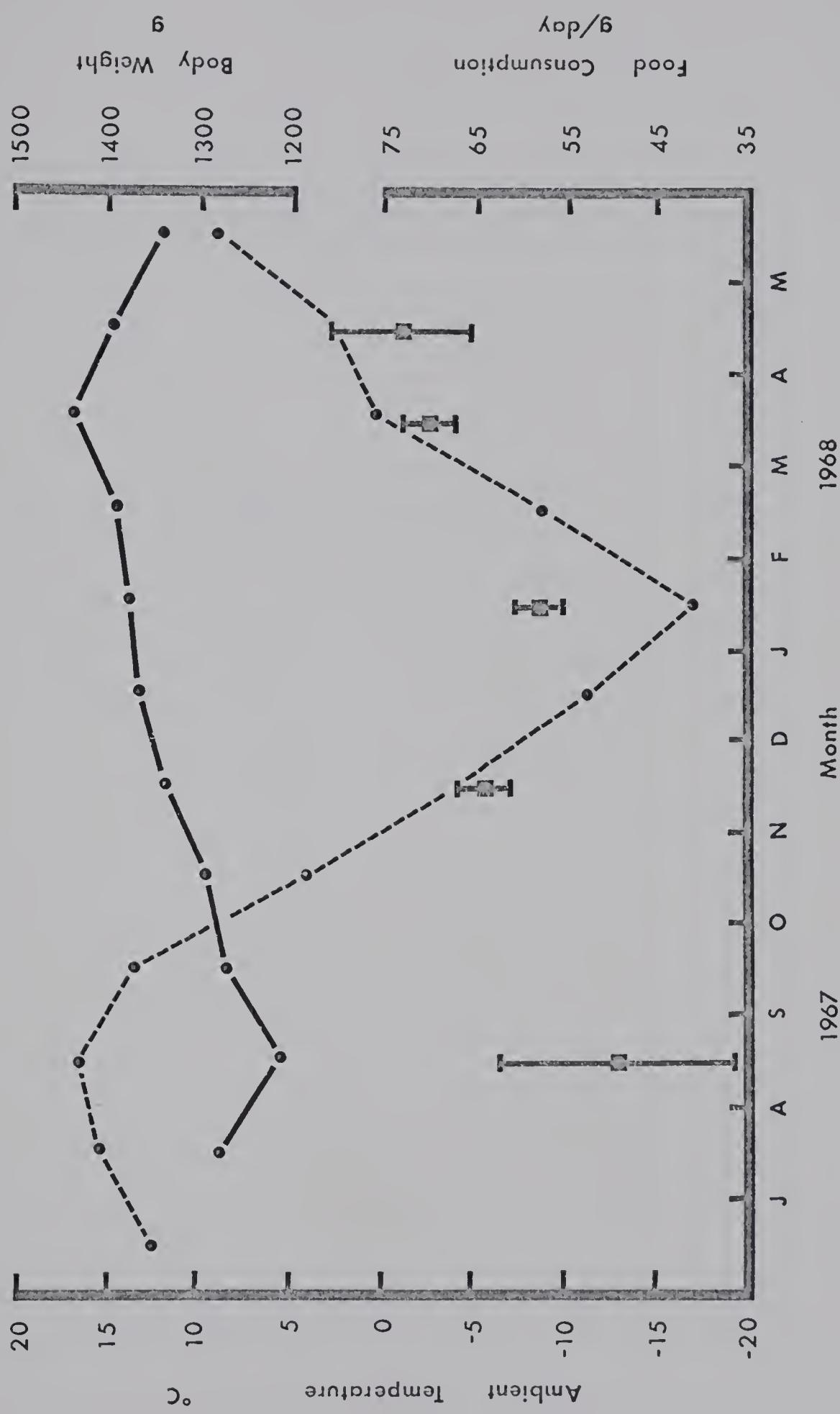


Figure 8. Mean monthly body weight (solid line), mean monthly ambient temperature (broken line), and average daily food consumption (squares) of female pheasants from June, 1967 to May, 1968. Vertical bars represent two standard errors of the mean.

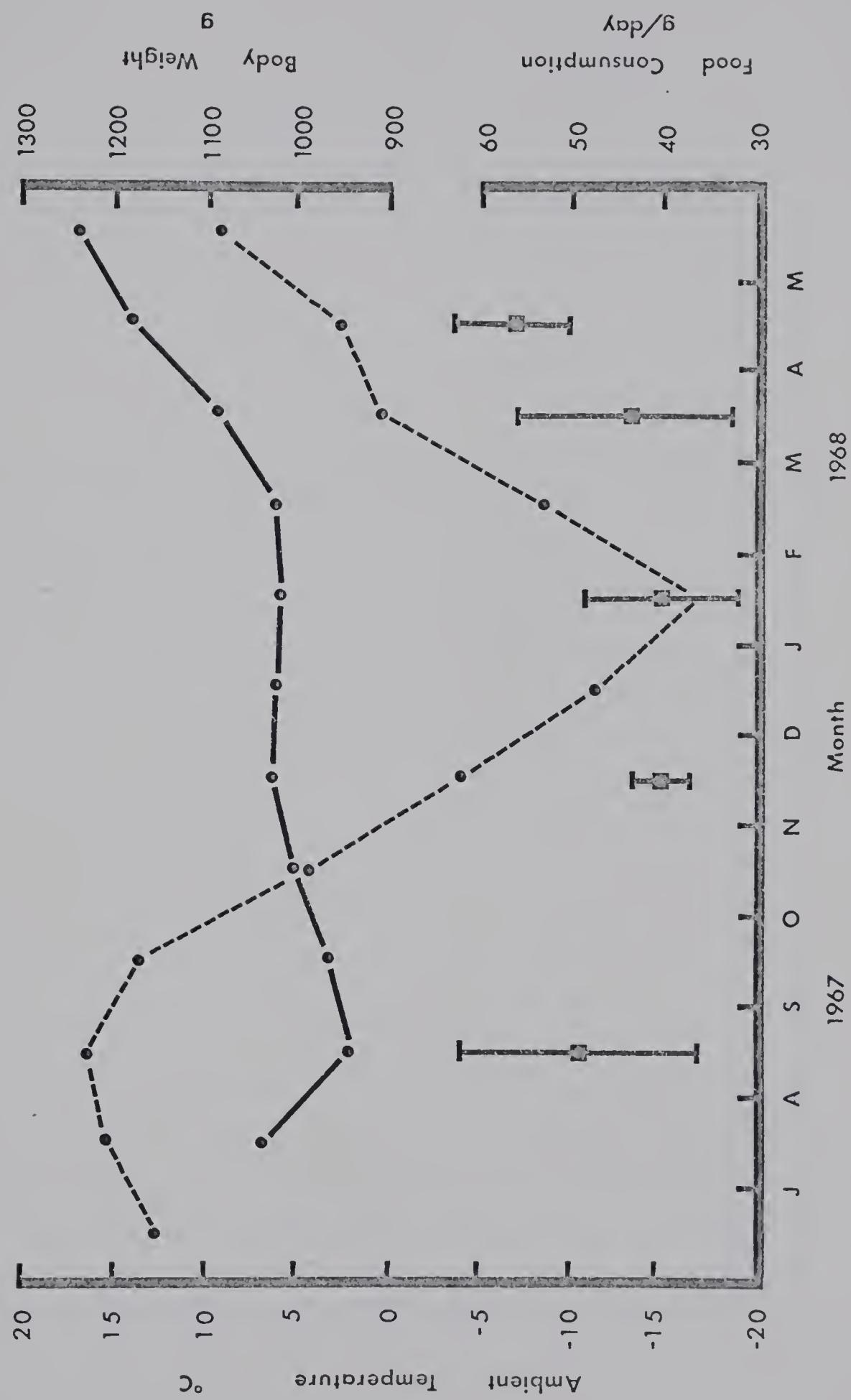


Figure 9. Mean monthly body weight (solid line), mean monthly ambient temperature (broken line), and average daily food consumption (squares) of partridges from June, 1967 to May, 1968. Vertical bars represent two standard errors of the mean.

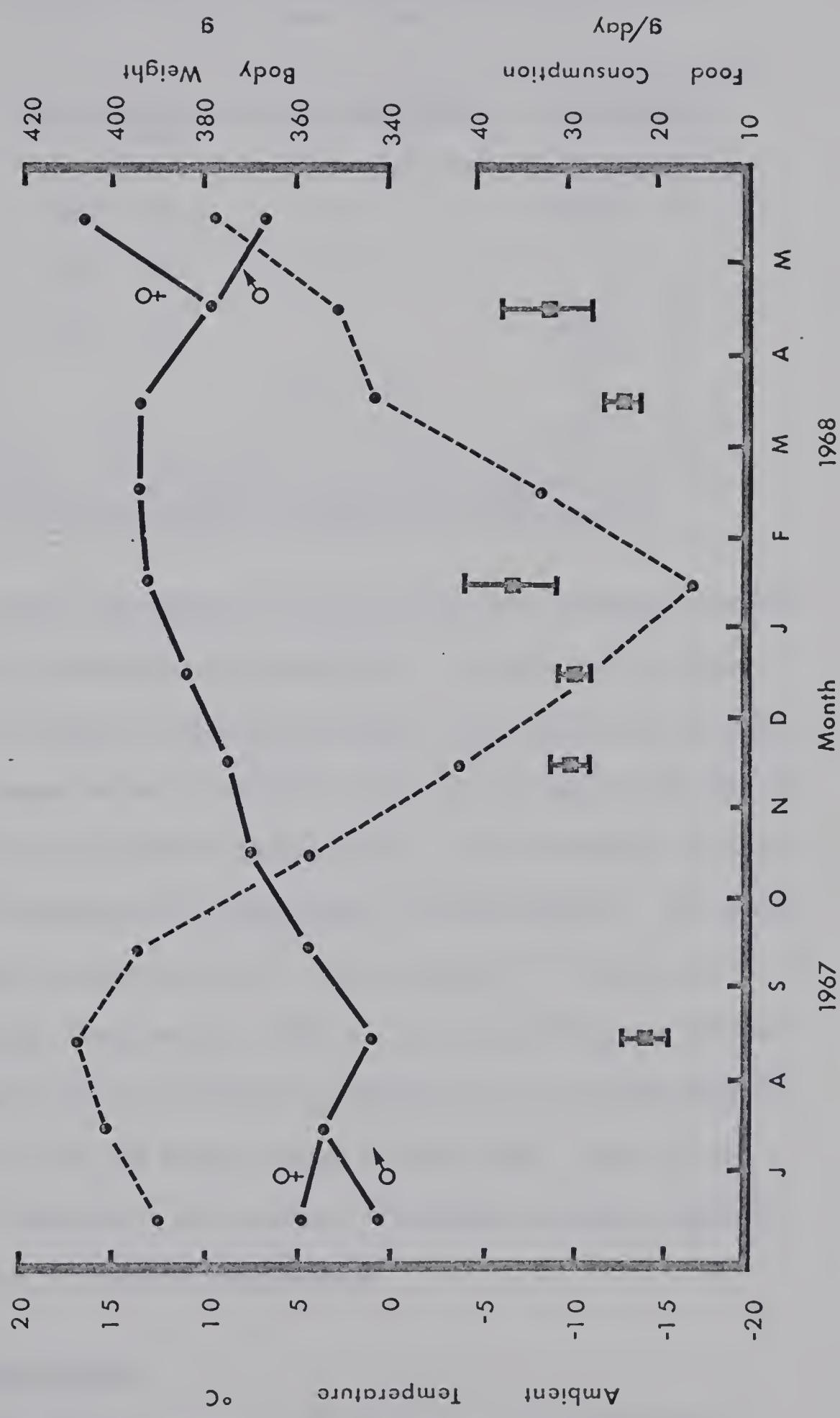


TABLE X. Student's *t* values and degrees of freedom used to determine significance of differences in monthly food consumption. Level of significance taken as < 0.05 .

Months	Male pheasants		Female pheasants		Partridges	
	<i>t</i>	DF	<i>t</i>	DF	<i>t</i>	DF
Aug.-Nov.	2.23	24	--		3.86	10
Nov.-Dec.					--	
Nov.-Jan.	3.01	36	--			
Dec.-Jan.					2.27	27
Jan.-Mar.	11.02	24	--		3.71	37
Mar.-Apr.	--		--		2.69	37
Jan.-Apr.			3.17	29		
Aug.-Jan.	--		--		4.77	23

Symbols used: *t* = Student's *t* value for significance; DF = degrees of freedom; dashes indicate non-significance.

Weights of male pheasants and male partridges indicate inverse relationship with environmental temperatures. Except for a spring weight-gain, the weights of female partridges (and also the hen pheasants, but to a lesser extent) parallel those of the males, and are inversely correlated with ambient temperatures. This inverse correlation is the result of increased fat deposition in cold weather. The added body fat provides insulation against the cold and is a ready source of metabolizable energy (Westerskov, 1965). The spring weight increase of female pheasants and partridges is probably due to the maturation of gonads, as both species began laying at this time. Some of the changes in food consumption may reflect variations in body weight as well as variations in ambient temperature.

Daily Energy Requirements

Tables XI and XII compare the daily energy requirements of

pheasants and partridges as predicted from the equation of Lasiewski and Dawson (1967), as observed from oxygen consumption, and as observed from gross food consumption. The values derived from oxygen consumption are also corrected to standard temperature and pressure. It should be noted that the values predicted from the equation and observed from oxygen consumption represent energy requirements within the thermoneutral zone only, whereas those derived from food consumption are at all ambient temperatures.

Only from the method of oxygen consumption is energy expenditure of pheasants greater in winter than at any other time of year. As determined from body weight and from food consumption, energy requirements for these birds are highest in spring. However, winter appears to demand the highest energy expenditure for partridges, as determined from all three methods. The energy requirement values derived from food consumption may be somewhat in error since my penned birds were supplied with food *ad libitum*. If food were not always readily available, as may be the case for wild birds, one would expect them to spend a great deal more energy in finding and obtaining it above that required for maintenance of homeothermy alone. Under such conditions winter energy requirements as determined from gross and/or net food intake may well be as great or greater than at any other time of year.

TABLE XI. Observed and predicted daily energy requirements of the pheasants.

	Energy requirements (kcal/bird/day)			
	August	November	January	April
Predicted from equation of Lasiewski and Dawson (1967); based on weight.	82.70	88.92	89.33	94.19
Observed from oxygen consumption, assuming 4.7 kcal/liter O_2 . Values also corrected.	91.50	86.21	100.64	77.61
Observed from gross food consumption.	207.27	222.41	212.68	275.82

TABLE XII. Observed and predicted daily energy requirements of partridges.

	Energy requirements (kcal/bird/day)			
	August	November	January	April
Predicted from equation of Lasiewski and Dawson (1967); based on weight.	37.07	38.19	39.90	38.73
Observed from oxygen consumption, assuming 4.7 kcal/liter O_2 . Values also corrected.	44.11	41.81	55.63	49.53
Observed from gross food consumption.	92.84	139.91	154.81	135.01

DISCUSSION

In a study on seasonal variation in stress resistance and survival in the hen pheasant, Kabat et al. (1956) utilized an "applied" stress of caging and starvation to test whether there is seasonal resistance variation and which of the naturally occurring physiological stresses caused the greatest decrease in resistance. The exposure of birds to a large range of temperatures, as in this project, can also be viewed as an applied stress, and the response, oxygen consumption, can serve as an index to changes in over-all resistance.

Kabat et al. (1956) found that resistance in hen pheasants was lowest in late summer when they had stopped laying. Their weight was then minimum, they had very low fat stores, and they were molting. As weight increased from fall to winter, survival also increased, and was at a maximum from February till April. On the commencement of breeding and egg production, mortality again increased. In considering winter survival the authors state that "...the demands of pheasants during the winter period are lower than during late spring and early fall. They are freed from the stress of molting and there is considerable storage of fat which not only provides a ready source of energy but also acts as an insulator which undoubtedly reduces the amount of fat burned for heat energy."

The physiology of pheasants and partridges as studied here also reflects such changes in stress patterns. Temperature-metabolism slopes and critical temperatures of both species as measured from oxygen consumption indicate low stress in winter. Food consumption for pheasants is also low at this time, but high for partridges. This would seem to

indicate that winter imposes more stress on partridges than on pheasants, especially since the former are smaller and lose heat more quickly. However, partridges increase feather insulation during winter. They also, in contrast to pheasants, have the habit of huddling in coveys to reduce heat loss. Winter survival for both species is thus the net result of some lowered stresses (molt, reproduction, low weight), some added stresses (low temperatures, snow which covers food) and changes in behavior and insulation.

The effect of multiple stresses on a bird during the year was clearly recognized by West (1960) when he attempted to plot the total energy expenditure of the Tree Sparrow, Spizella arborea. Energy required for standard metabolism, chemical thermoregulation, specific dynamic action of food assimilation, and the securing of food and water was termed "existence energy". Added to this was "productive energy", which included that required for the deposition of fat, spring and fall molts, reproduction, and migration. These latter stresses occur from March to November and result in the energy requirements during this period being substantially greater than those during the winter period, from November to March. Finally, West added a "cost of free existence", which has not been measured, but which he concludes might make the total energy intake more nearly the same throughout the year. Except for this last step, West's conclusions on the yearly energy budget of the Tree Sparrow closely resemble the results found in this study for pheasants and partridges. Low temperatures during winter demand extra energy for maintaining homeothermy and for finding food, especially if it is covered with snow, but added stresses during the spring, summer, and fall months

require an even greater energy expenditure, and concomitant with this, lower the bird's resistance to other stresses.

Therefore, average winter temperatures per se would not be expected to limit either the numbers or the northward distribution of pheasants and partridges in Alberta. However, optimum conditions of temperature together with humidity (plotted as the "climograph") have been suggested as necessary for survival of the species, especially during oviposition and growth of the young (Graham and Hesterberg, 1948; McCabe and Hawkins, 1946). With respect to winter survival only, Lyon (1954) considers the critical factor to be suitable roosting habitat. Feeding habits must also be considered. Both species feed largely on waste grain and weed seeds throughout the year (Bent, 1932; Westerskov, 1966). Since they change neither their diet nor their ground-feeding habit during the winter, this means they must dig through snow to feed during winter months. At this time excessively deep snow or the development of a hard crust on its surface may result in great casualties (Formozov, 1963). Survival of pheasants and partridges results, then, from a combination of many factors, including suitable agricultural habitat for food, nesting, and roosting, favorable weather conditions during times of stress, and satisfactory snow conditions during winter. Further study on all these factors is necessary to obtain a more thorough knowledge of the environmental physiology of these birds.

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APPENDIX I

Oxygen consumption in relation to ambient temperature, for the pheasants. Numbers in brackets refer to number of birds involved.

Temp. (°C)	Oxygen consumption (cc O ₂ /g/hr)			
	Summer (6)	Fall (12)	Winter (11)	Spring (8)
40	1.10			
	0.87			
37	0.69			
35	1.04			
33	0.77	1.29		
32	0.56			
30	0.76		1.12	
28		0.87	0.97	
27		0.67		
26	0.77			
	0.95			
25			0.60	0.51
23				0.51
22	0.84		0.81	0.50
	0.88		0.72	
	0.78			
21	0.84		1.19	0.46
	0.84			0.84
20		0.81		
		0.51		
18				0.51
17		0.61	1.08	
			0.95	
16			0.65	
15				0.84
14			0.60	0.62
13	1.03		0.72	0.63
12	0.91	1.05	0.74	
11	1.00		0.82	
10	0.97			1.04
9			0.90	0.51
8		0.85		
7			1.18	0.84
			1.21	
6			0.93	0.79
			0.71	
5		1.05		
		0.79		
4			0.79	0.55

APPENDIX I (continued)

Temp. (°C)	Oxygen consumption (cc O ₂ /g/hr)			
	Summer	Fall	Winter	Spring
3	1.18	0.87		0.64
		1.07		
2	1.31	0.83	1.06	
	0.98			
1	1.12	0.65	1.07	0.68
			1.03	
			1.19	
- 1			1.28	1.06
- 3				1.11
- 5	0.93	1.34		0.96
		1.07		
- 6	1.45	1.17	1.11	
	1.22			
- 7		0.89	1.47	0.79
			0.74	
				1.35
- 8			0.91	
- 9			0.75	
-10	1.54			1.26
	1.80			
-11		1.08		0.92
-13		1.21	0.91	
		1.02		
-14	1.00	1.43	0.75	0.95
	1.84			
-15		1.48		1.28
-16		1.29		1.36
-17	1.35	0.94	1.69	1.44
	1.43			
-18	1.87		0.49	1.29
			0.91	
-19		1.05		1.42
-20	1.80	1.49		
	1.35			
	1.77			
	2.13			
-21			0.84	1.42
-22	2.39		1.22	
			1.36	
-23	1.97			
-24	2.01			
-25	1.76		0.75	
	1.70			
-26		1.61	0.98	1.77
		1.56	0.49	
			0.74	

APPENDIX I (continued)

Temp. (°C)	Oxygen consumption (cc O ₂ /g/hr)			
	Summer	Fall	Winter	Spring
-27	1.80	1.37	0.80	
-28	1.46	1.68		
	1.70			
-29	2.09			1.60
-30			0.49	1.53
-31	1.77	1.73	0.98	
			0.91	
-32		1.68	1.12	
-33	1.73			1.47
-37			0.91	

APPENDIX II

Oxygen consumption in relation to ambient temperature, for the partridges. Numbers in brackets refer to number of birds involved.

Temp. (°C)	Oxygen consumption (cc O ₂ /g/hr)			
	Summer (8)	Fall (4)	Winter (4)	Spring (4)
40	1.42			
39	1.49			
38	1.17			
35	1.19			
	1.54			
31	1.23			
30	1.20			
	1.17			
29	1.54			1.71
27	1.12			1.28
26	0.96	0.85		1.32
	1.20			
25	1.29			1.43
24			1.46	1.51
			1.56	
23	1.48		1.52	
	1.17			
22	1.32		1.47	
	1.16			

APPENDIX II (continued)

Temp. (°C)	Oxygen consumption (cc O ₂ /g/hr)			
	Summer	Fall	Winter	Spring
21	1.44		1.72	1.38
	1.49		1.45	0.87
	1.23		1.39	
20			1.84	
19	1.29			1.72
18	1.16			
	1.21			
17			1.52	1.28
			1.72	
16		0.85		1.48
				1.51
14	1.20			
13			1.47	1.03
12	1.34	1.51	1.46	1.38
	1.63	1.06	1.63	
			1.56	
11		1.79	1.79	
			1.92	
10	1.60		1.56	
9	1.73			1.72
	1.99			
8	1.20	1.02		1.28
7	1.75			1.66
6			1.04	
5	1.62		1.52	1.90
3	1.96	1.30	1.63	
2		1.96	1.48	1.52
			1.56	1.28
1		1.24	1.62	
0	2.10			2.40
	1.27			
	1.84			
	2.09			
	1.99			
- 1	1.44	1.24	1.39	
			1.94	
			1.47	
			1.46	
- 2			2.25	1.87
				1.45
				1.98
				1.36
- 3	2.25			2.26

APPENDIX II (continued)

Temp. (°C)	Oxygen consumption (cc O ₂ /g/hr)			
	Summer	Fall	Winter	Spring
- 4				2.26
- 5	1.77			
	1.58			
- 6	2.39	1.20		
- 7	1.89	1.90		1.99
	1.65			1.16
				2.59
- 8	2.15	1.68	2.27	
	2.12		1.64	
			1.52	
- 9		1.86	1.97	
		1.77		
-10	1.62		1.90	1.37
				1.82
-11	1.19		1.56	
-13			1.91	2.31
-14			1.92	1.57
-15	1.94			
-16	2.44			2.79
	1.19			
-17	2.60			
-18	2.36		2.48	
-19		2.50	2.61	
-20	2.83	2.22	2.07	
	2.08			
-21				1.37
				2.56
-24		2.74	1.90	
-25	2.65			
	1.13			
-26			1.91	3.15
-27			2.08	
-28	2.72			1.37
	1.94			
-29	2.60			
-30	1.18			
	2.36			
-31		2.56		
		2.34		
-32	2.54		1.75	3.07
-33		3.02	1.92	
-34		3.00		
-36	2.96			
	2.90			

APPENDIX III

Food consumption in relation to daily mean ambient temperature, for male and female pheasants and for partridges.

Date	Food consumption (g/day)			Mean Temperature	
	Male ph.	Female ph.	Part.	(°F)	(°C)
Aug.					
(1967)					
1	29.0		20.8	57	13.9
2	50.0		20.8	59	15.0
10	42.0		23.5	67	19.4
11	55.0		18.6	67	19.4
12	69.0		26.0	64	17.8
Nov.					
9	61.7	43.4		34	1.1
10	61.7	43.4		29	-1.7
11	64.7	29.0		19	-7.2
12	64.7	29.0		15	-9.4
13	61.7	40.5		17	-8.3
14	61.7	40.5		20	-6.7
15	69.4	54.0		41	5.0
16	69.4	40.5		40	4.4
17	69.4	40.5		33	0.6
18	86.8	57.9		27	-2.8
19	69.4	49.2		26	-3.3
20	69.4	49.2		30	-1.1
21	54.0	40.5		29	-1.7
22	54.0	40.5		40	4.4
23	57.9	34.7	25.3	32	0.0
24	57.9	34.7	25.3	33	0.6
25	65.6	34.7	27.0	17	-8.3
26	65.6	34.7	27.0	4	-15.6
27	61.7	36.0	30.4	8	-13.3
28	61.7	36.0	30.4	12	-11.7
29	61.7	36.0	30.4	13	-11.1
Dec.					
4			31.5	28	-2.2
5			31.5	23	-5.0
6			31.5	19	-7.2
7			33.8	13	-10.6
8			33.8	6	-14.4
9			25.3	24	-4.4
10			25.3	34	1.1
11			27.0	26	-3.3
12			27.0	19	-7.2
13			27.0	11	-11.7

APPENDIX III (continued)

Date	Food consumption (g/day)			Mean Temperature	
	Male ph.	Female ph.	Part.	(°F)	(°C)
Jan. (1968)					
6	24.6		19.1	-25	-31.7
7	24.6		19.1	-17	-27.2
8	55.9	17.9	46.8	-15	-26.1
9	55.9	17.9	46.8	-19	-28.3
10	55.9	17.9	46.8	-18	-27.8
11			31.9	-24	-31.1
12			31.9	6	-14.4
13	83.8	61.2	57.4	5	-15.0
14	83.8	61.2	57.4	9	-12.8
15	43.7	30.6	38.3	17	-8.3
16	43.7	30.6	38.3	27	-2.8
17	65.6	49.7	38.3	23	-5.0
18	65.6	49.7	38.3	32	0.0
19	62.8	61.2	31.9	23	-5.0
20	62.8	61.2	31.9	22	-5.6
21	65.6	38.3	28.7	28	-2.2
22	65.6	34.0	25.5	21	-2.8
23	65.6	34.0	25.5	42	5.6
24	65.6	34.0	25.5	35	1.7
Mar.					
1	78.7	66.5	19.0	38	3.3
2	78.7	66.5	19.0	39	3.9
3	72.4	38.0	12.7	39	3.9
4	72.4	38.0	12.7	44	6.7
5	72.4	38.0	12.7	43	6.1
6	65.1	25.3	19.0	43	6.1
7	65.1	25.3	19.0	38	3.3
8	76.0	14.3	31.7	27	-2.8
9	76.0	14.3	31.7	27	-2.8
10	68.8	19.0	19.0	21	-6.1
11	68.8	19.0	19.0	27	-2.8
12	76.0	23.8	38.0	23	-5.0
13	76.0	23.8	38.0	19	-7.2
14	67.9	76.0	38.0	21	-6.1
15	67.9	76.0	38.0	28	-2.2
24	70.6	95.0	23.8	42	5.6
25	70.6	95.0	23.8	40	4.4
26	54.3	42.8	19.0	41	5.0
27	54.3	42.8	19.0	39	3.9

APPENDIX III (continued)

Date	Food consumption (g/day)			Mean Temperature	
	Male ph.	Female ph.	Part.	(°F)	(°C)
Apr.					
4	49.4	63.3	33.3	37	2.2
5	49.4	63.3	33.3	39	3.9
6	76.0	57.0	50.7	38	3.3
7	60.8	47.5	38.0	36	2.2
8	60.8	47.5	38.0	36	2.2
9	67.0		33.3	48	8.9
10	76.0		33.3	38	3.3
11	59.1	38.0	25.3	32	0.0
12	66.5	28.5	50.7	17	-8.3
19	57.0	57.0	28.5	38	3.3
20	57.0	57.0	28.5	35	1.7
21	85.5	71.3	25.3	31	-0.6
22	85.5	71.3	25.3	35	1.7
23	101.3	71.3	42.8	45	7.2
24	101.3	71.3	42.8	44	6.7
25	104.5	57.0	19.0	43	6.1
26	71.3	52.3	19.0	41	5.0
27	71.3	52.3	19.0	48	8.9
28	85.5		19.0	51	10.6

APPENDIX IV

Mean monthly ambient temperatures and mean monthly body weights of male pheasants, female pheasants, and partridges, from June, 1967 to May, 1968.

Month	Mean ambient temp. (°C)	Mean body wt. of male ph. (g)	Mean body wt. of female ph. (g)	Mean body wt. of part. (g)
June	12.8			360-females 343-males
July	15.6	1280	1040	355
August	16.7	1213	943	344
September	13.9	1273	963	358
October	4.4	1293	1003	370
November	-3.9	1340	1030	375
December	-11.1	1372	1028	384
January	-16.7	1382	1020	393
February	-8.3	1399	1023	394
March	0.6	1443	1088	394
April	2.8	1401	1185	378
May	9.4	1350	1245	406-females 366-males

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